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TYPES OF NEUROMUSCULAR MECHANISM IN SEA-ANEMONES.

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(Read April 15, 1916.)

Sea-anemones possess at least four systems of organs by which they react to environmental changes: the glandular system, especially the mucous glands, the ciliary system, the nematocyst system, and the muscular system. Of these the first three are strictly local in their responses in that they become active only in the exact regions where they are stimulated. Moreover they remain normally responsive in animals that have been so completely anesthetized with magnesium sulphate or chloretone as to exhibit no nervous activity. Hence there is good reason to assume, notwithstanding the opinion held by some of the older workers, that none of these three systems are under nervous influence. The fourth system, the muscular, is well known to be controlled by the nervous system of these animals. In the common New England sea-anemone, *Metridium marginatum*, the neuromuscular mechanism includes at least thirteen muscles or groups of muscles. Two of these are ectodermic, (1) the longitudinal muscle of the tentacles and (2) the radial muscle of the oral disc; the remaining eleven are entodermic and are as follows: (3) the circular muscle of the tentacles, (4) the circular muscle of the oral disc, (5) the circular muscle of the œsophagus, (6) the sphincter, (7) the circular muscle of the column, (8) the circular muscle of the pedal disc, and the five mesenteric muscles, namely, (9) the basilar muscles, (10) the longitudinal mesenteric muscles, (11) the transverse mesenteric muscles, (12) the parietal muscles, and (13) the longitudinal muscles of the acontia or nettling filaments.

The nervous mechanism by which these muscles have long been supposed to be brought into action is a network of neurofibrils and the like which permeates the deeper regions of the ectoderm and the

entoderm and the two parts thus established are believed by many investigators to be continuous in the œsophageal region where ectoderm and entoderm are confluent. According to O. and R. Hertwig (1879-1880), Wolff (1904), and others this nervous network is more extensively developed in the oral disc than elsewhere and constitutes there a primitive central nervous organ. Grošelj (1909), however, believes that this centralization is in the œsophagus. Many other workers (Nagel, 1892; Loeb, 1895; Parker, 1896, Havet, 1901; Bethe, 1903; Jordan, 1908, 1912) maintain that this network is not sufficiently centralized anywhere in the actinian's body to justify the statement that the nervous system of the sea-anemone is other than a diffuse one.

Vigorous stimulation of almost any part of the surface of a sea-anemone is commonly and quickly followed by the complete contraction of the whole animal; and the response is so protracted that actinian muscle has come to be regarded as specially adapted to tonic contraction rather than to the rapidly changing phases of contraction and relaxation so characteristic of the muscles of the higher animals. This view has gained such strength that von Uexküll (1909) and Jordan (1909, 1908, 1912) have come to look on these muscles as almost exclusively tonus muscles and Jordan (1908) especially has gone so far as to deny to sea-anemones the possibility of muscular reflexes such as are so usual among the more differentiated animals. An adequate examination of the muscular activities of sea-anemones will show, I believe, that these animals have a much more complex muscular mechanism than has been previously suspected and that at least three and possibly four types of muscular activity can be distinguished in them.

The simplest of these types is that seen in the longitudinal muscle of the acontium. This muscle can be brought into action by the direct application of an appropriate mechanical or chemical stimulus. Its contraction changes the acontium from a long straight filament into a loosely twisted, spiral one. This response is strictly local in relation to the stimulus and does not spread appreciably from the region stimulated to other parts. It is as well pronounced in acontia that have been in an anesthetizing solution (magnesium sulphate or chloretone) long enough to abolish all nervous activity in other parts

of a sea-anemone as it is in normal acontia. I therefore conclude that the acontial muscle is one that is normally stimulated directly and that it is without nervous connections. In this sense it represents primitive muscle unassociated with nervous tissue as has already been identified in sponges (Parker, 1910).

A second type of muscle is that seen in the circular muscle of the column of *Metridium*. When a portion of the column of this animal is fully anesthetized with magnesium sulphate, a mechanical stimulus will not elicit from it the usual contraction of the animal as a whole, but a ring of contraction will extend more or less completely around the column. When the column is not anesthetized and the sea-anemone is vigorously fed, this muscle exhibits peristaltic movements which apparently depend upon nervous activity. The circular muscle of the column, therefore, seems to be a muscle open to direct stimulation and also under the control of nerves. In this respect it resembles the sphincter pupillæ of the vertebrate eye which responds not only to nerve impulses but also directly to light.

A third type of muscular mechanism in sea-anemones is seen in the longitudinal muscles of the mesenteries. These contract when almost any part of the surface of a *Metridium* is stimulated, but they fail to respond when the animal is deeply anesthetized. Hence I conclude that they are primarily controlled by nerves. Under ordinary stimulation their action is profound and lasting and is one of the most important elements in the general contraction of the animal as a whole. It is their activity that in large part has given grounds to the idea that the actinian muscle is specialized almost exclusively on the side of its tonicity.

Finally a fourth type of muscle mechanism is that seen in the transverse muscles of the mesenteries, particularly of the complete mesenteries. When food juice is discharged on the tentacles or lips of an expanded *Metridium*, the transverse mesenteric muscles contract and thus open the œsophagus preparatory to what under normal circumstances would be the swallowing of the food. On withdrawing the stimulus these muscles quickly relax and the œsophagus closes. This reaction is so definite and precise in its

relation to the stimulus and so invariable in its occurrence that it must be regarded as a true reflex and as an example of such an operation it certainly compares very favorably with what is often seen in many of the higher animals.

The muscular reactions of the sea-anemones are then by no means all of a kind, but range from direct muscle responses of a most primitive character to true reflexes. The more complex operations of these animals such as food-taking, creeping, and so forth, are not to be regarded as the result of the action of a relatively uniform neuromuscular mechanism, but depend upon some combination of the various types of muscular or neuromuscular activity possible to these animals. These operations are often extremely complex and call for a high degree of coördination and yet this coördination is almost entirely of local origin, for an isolated tentacle will react to food almost exactly as an attached one does and the pedal disc, even after the oral disc has been cut away, will creep in a fashion indistinguishable from that of a whole animal. There is therefore good grounds to agree with those who maintain that the nervous system of the sea-anemone is essentially diffuse lacking obvious centralization.

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